PLANT GEOGRAPHIC STUDIES ON DIPTEROCARPACEAE IN MALESIA¹

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The primary lowland forest of tropical Southeast Asia west of Wallace's Line have the peculiar feature that they are dominated as regards the numbers of emergent trees and volume of timber by a single family, the Dipterocarpaceae. The timber produced by trees belonging to this family is often sold in the United States under the rather misleading name Philippine mahogany. Renewed interest in this family among scientists and environmentalists in the U.S.A. stems from the studies of military forest destruction in Vietnam, and the opening up of large new American timber concession holdings in Indonesian Borneo and Sumatra. There is an awareness that the Dipterocarpaceae are a unique object for biosystematic and plant geographic study besides being the most valuable renewable natural resources of extensive areas of Southeast Asia (Foxworthy, 1946; Slooten, 1961; Ashton, 1969b; Jong & Lethbridge, 1967). They are, as regards sizes of trees, biomass and number of species, the most successful family among all Angiosperm families in Southeast Asia. The unexploited forests of Borneo and Sumatra represent a fortune of many billions of dollars in timber value. From a purely scientific point of view, the Dipterocarpaceae are extremely interesting because they occur in areas which have had a relatively stable geology since the Cretaceous, probably the time of their origin. Since that time they have spread over Southeast Asia and over Africa; possibly they occur in disguised forms also in the American tropics as plants now considered to belong to Tiliaceae. In their leaf forms and indumentum they show Malvalean characters. The flowers of the African Monotes have short androgynophores, and their barks have slime ducts as in some Tiliaceae. The Dipterocarpaceae proper have resin canals in their woods and the flowers have calyx lobes which enlarge and develop into wings on the ripening fruit. Stamens occur in 5 whorls of 3 or in multiples of 15.

Because of the *dispersal* of the fruits by wind over distances in general not further than up to half mile, we can use the Dipterocarpaceae as tracers of old land connections. Because large areas of Malaya, Sumatra, and Borneo, the

¹This paper was originally written for the 19th Annual Systematic Symposium supported by the National Science Foundation, and the Missouri Botanical Garden, 20–21 October, 1972, as part of a seminar on "Systematic studies in the lowland tropics." I express my great appreciation to Dr. Peter Raven for stimulating discussions leading to this Symposium topic. Prof. Dr. C. G. G. J. van Steenis, Editor, Flora Malesiana, supplied me promptly with information on Sumatran Dipterocarpaceae and Dr. F. R. Fosberg (Smithsonian Institution, Washington, D. C.) gave helpful suggestions for the editing and publishing of this paper. The cooperation of Weyerhaeuser Company with reconnaissance flights over logging areas in Sabah is also gratefully acknowledged.

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ANN. MISSOURI BOT. GARD. 61: 806-818. 1974.

MEIJER-PLANT GEOGRAPHIC STUDIES

807



FIGURE 1. Flowering lowland dipterocarp forest north of Segama River, near Lahad Datu, Sabah. Note the usual distance between flowering trees belonging to the same species.

main center of the family, were until recently relatively undisturbed, we can study the patterns of distribution of species pretty closely. These patterns can be related to taxonomic affinities of species, their ecological adaptations, and

their flower and fruit biology. Hopefully we can learn in this way something about speciation in tropical rain forests (Ashton, 1969b). However, there is little time left to tackle comprehensive biosystematic studies of this family because the rate of disappearance of primary rain forests in Southeast Asia is far outstripping the very feeble attempts made for botanical exploration.

A family like the Dipterocarpaceae needs to be studied in the field by keen alert young forest botanists who are technically well equipped with good documentation methods, who also know how to use tree climbers and who possess extreme perseverance. Differences between species of Shorea, now amounting to 164 species, are often very minute and their study can be tedious. A lot of sterile herbarium material stays a long time as undetermined in file cabinets. Rapid progress with their identification can only be made by specialized botanists who go out in the field and who at the costs of much sweat and labor get themselves familiar with these trees in all their stages, from seedling to adult, with flowers, fruits, sterile branches and fallen leaves (Fig. 1). This takes a lot of time and patience. Foresters are often not disposed to make such detailed careful field studies and after they get training they often tend only to look at the known species and pass by the unknown or fit them together with species they pretend to know. The local names are often very confused and a bad guide in genera with minute differences between species. A professional field taxonomist always quickly outgrows the local experience of so-called tree-experts. The knowledge about the dipterocarps of Indonesia has been accumulating very slowly though steadily by collections brought together by foresters and worked

up by van Slooten, who was mainly an herbarium botanist. There are stories that when he once entered a forest in Borneo he could not recognize the Dipterocarps (Dilmy, personal communication). The herbarium collections often come from areas where in 100 square kilometers not more than 5–10 plants have been collected—like most of lowland Sumatra, an island about the size of California. That whole area has never had a full time professional field taxonomist who was specialized in the Dipterocarpaceae and without doubt, scores of species still have to be discovered there. I made a few expeditions in the lowland

Dipterocarp forests of East Central Sumatra during 1955–1956, but I am sure that with my present experience I would get far more out of it.

Intensive work has been done during the last 15 years in former British Borneo, Sarawak, Brunei, and Sabah by Wood, Ashton, Anderson, and myself. From this resulted the description of 88 species new to science. There is no reason to believe that Sarawak is richer in Dipterocarpaceae than western Indonesian Borneo with collection density of seven specimens per 100 square kilometers. Consequently we can conclude that a lot more intensive field work should be done before we have a more complete picture of speciation and evolution in this family. It is hoped that the U.S.A. can assist Indonesia not only in exploiting its natural resources by logging big concession areas and buying about half of the Dipterocarp timber exports from Japan, but also in exploring and conservation. If no adequate botanical reserves are set aside in Borneo and Sumatra, we will be faced with irreparable loss of one of the most interesting and valuable gene pools of trees in the world. Intensive training courses and exploration work will be needed here as well as in the Philippines. Dipterocarp collections in the National Museum in Manila are totally unrepresentative. It is a fact that these forests can be exploited without bothering too much about the niceties of species identification though intensive research in Malaya by Symington (1943) and Desch (1957) and in Sabah by Wood and Meijer (1964) and Burgess (1966) certainly has assisted to standardize timbers and their uses on the buyers' markets (mainly Japan). It is essential now to accompany the new opening up of forests in Indonesian Borneo (Kalimantan) and Sumatra with renewed field work on the Dipterocarps and to assure that areas are not being overlogged or swept away in conversion into useless grasslands, which already cover five million hectares in Sumatra (Dilmy, 1960). It has been shown in Sabah that lowland Dipterocarp forests can be logged selectively on a sustained yield basis and that this type of landuse is in many areas far preferable to so-called conversion into agricultural lands because the soils of tropical lowlands are not permanently productive without tree cover, except under irrigation. A strong case was made in Sabah for a permanent Forest Estate on the East Coast by a team of United Nations Special Fund researchers. Similar cases could be made in tropical America and tropical Africa.

SPECIATION AMONG DIPTEROCARPS IN BORNEO

Compared with other parts of Southeast Asia, Borneo is at present undoubtedly the center of development of the Dipterocarpaceae. Sarawak with about

MEIJER-PLANT GEOGRAPHIC STUDIES

809

247 species (Ashton, 1969) has about the same size as Malaya with 160 species (Symington, 1943). Sabah, about the size of Virginia but still not fully explored, has about 160 known species (Wood & Meijer, 1964), tiny intensively explored Brunei has 153 (Ashton, 1963). There is now growing evidence that the western part of Borneo has a greater species density for Dipterocarps than the Southeast and South. This can possibly be explained by longer geological stability. It is the so-called central core of Palaeozoic and early Mesozoic rocks, exposed since the Cretaceous. Other portions of that old Sunda Shield area are found in Malaya and Sumatra, and around that we find a mantle of late Mesozoic and Tertiary rocks in great geosynclinal formations (Kirk, 1968). After an early phase of volcanism in the Upper Cretaceous, of which rocks are exposed in eastern Sabah, around Darvel Bay, there was another phase in the Miocene with uplifting of the ultrabasic mountains in the Labuk area (Kirk, 1968). During the same time there must have been a high mountain range along the Crocker range, the northern continuation of the watershed between Sarawak and Kalimantan, according to palynological data studied by J. Muller (1966).The occurrence of Dipterocarpaceae in Africa, India, as well as Malesia, and their possible relationship with some rare or undescribed forms in Latin America suggest that the roots of this family go back to the area of the possible Gondwanic origin of pan-tropical lowland families. However, it seems too early to be sure about the center of origin of the various genera. Facts so far established are that in Borneo the fossil records of pollen and macro-fossils of the genus Dipterocarpus go back to the Oligocene (Muller, 1964, 1970), in Assam and India up to the Himalayan foothills to the Miocene (Lakhanpal, 1970). Fossils also have been found in the Tertiary of Egypt and Somaliland (Lakhanpal, 1970). Merrill (1923) reports Pliocene leaf prints of three species from Luzon identified with species now living in the Philippine Archipelago. A number of widespread genera and species may have originated over the late Cretaceous or early Tertiary land connections reaching from Malesia to India. Shorea, Dipterocarpus, Vatica, and Hopea all range from Ceylon to Malesia. The following species reached out beyond Borneo:

Dipterocarpus grandiflorus-Burma, Thailand, Malaya, Sumatra, Borneo, Philippines.

Dipterocarpus gracilis-Burma, Thailand, Malaya, Sumatra, Java, Borneo, Philippines.

D. kerrii-Andamans, Burma, Thailand, Malaya, Borneo. D. hasseltii-Siam, Malaya, Sumatra, Borneo, Philippines. Anisoptera costata—Northwest Thailand, Malaya, Sumatra, eastern half of Borneo, Moluccas, New Guinea. Shorea gratissima—Tenasserim, Siam, Malaya, Borneo. Shorea guiso-Indochina, Siam, Malaya, Borneo, Philippines. Vatica mangachapoi-Malaya (high hills in the North), Borneo, Philippines (all areas) according to Ashton (1964).



FIGURE 2. Shorea maxwelliana near Gravel pit, Sungai Manila Road, Sandakan, Sabah. Flowers and fruits were collected from this tree by the use of the native ladder construction. Authentic wood sample was taken for timber study.

MEIJER-PLANT GEOGRAPHIC STUDIES 1974]

At least 78 species occurring in Sumatra have been found also in Malaya and at least 55 species are shared between Sumatra and Borneo. The most prominent species shared among Malaya, Sumatra, and Borneo are Dryobalanops aromatica, the so-called camphor tree, Dipterocarpus lowii, D. palembanicus, D. verrucosus, and Shorea leprosula. Besides, there is a rather considerable group of species which seem to have spread from Borneo to Malaya and some beyond that to Thailand:

Shorea gratissima S. faguetiana S. lamellata S. gibbosa S. multiflora S. kunstleri S. teysmanniana S. exelliptica S. flava

Dipterocarpus sarawakensis D. humeratus D. oblongifolius D. acutangulus Anisoptera laevis Cotylelobium malayanum Hopea dyeri H. montana H. nervosa H. nutans

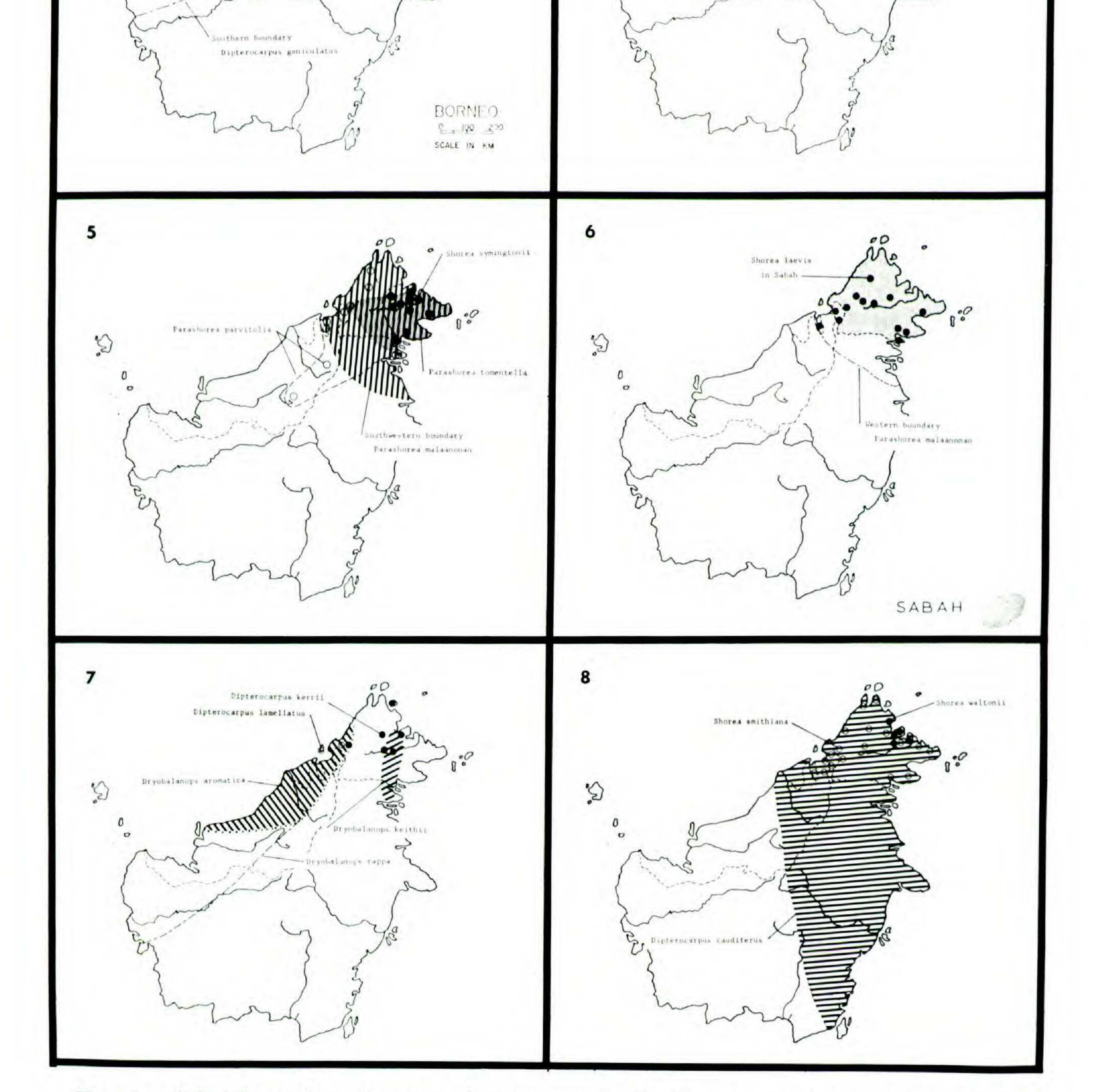
Towards the east there are species which link Borneo with the Philippines, and most of these have their Bornean center in Sabah:

Dipterocarpus warburgii Vatica mangachapoi Parashorea malaanonan

Shorea almon S. seminis

The farthest link between Borneo and islands east of it is through Vatica papuana. However, that could be a case of distribution of fruits in coastal drift. So far no experimental proof has been given for this, though Vatica papuana tends to grow on clayish soils at the inner side of mangroves. The very remarkable fact that the Ceylonese Vateria copallifera is narrowly related with Vatica papuana has been overlooked a long time (Meijer, 1972). There are also a number of species in Borneo which are endemic. Some of these seem to occur over the whole island, like Shorea virescens.

Others occupy more or less the northern half, others the southern, others only occur in the southeast (Shorea smithiana), still others only in the northeast. Quite a few species are restricted to the area northwest of the Crocker Range (Shorea albida, Shorea slootenii, Dryobalanops rappa, Upuna borneensis, and scores of others). There are 8 species endemic to Sabah: Vatica maritima, Shorea leptoderma, S. waltonii, S. symingtonii, S. hypoleuca, S. kudatensis, Hopea argentea, and Dipterocarpus pachyphyllus. Most of these species are locally sufficiently abundant to be considered vigorous young species, like Shorea waltonii, S. kudatensis, and Dipterocarpus pachyphyllus. Parashorea tomentella and Dryobalanops lanceolata occur mainly in Sabah and adjacent Indonesian Borneo, and within their distribution areas they are sufficiently common to form substantial volumes in the export timber market.



FIGURES 3-8. Examples of species distributions inside Borneo.—3, 4, 5, and 8. Areas of species centered in or around Sabah (lightly shaded in Fig. 6).—6. Scattered distribution of *Shorea laevis* in Sabah. Farther south in East Malasian Borneo this species is far more frequent. It also occurs in Malaya.—7. Only the scattered distribution of *Dipterocarpus kerrii* inside Sabah is illustrated.

MEIJER-PLANT GEOGRAPHIC STUDIES

813

Detailed analysis of vegetation types has shown that there is a lot of diversity according to ecological preferences. The most remarkable is the contrast in Dipterocarp flora between sandstone, shale, and basaltic areas dominated by a concentration of Parashorea malaanonan, P. tomentella, Dryobalanops lanceolata, and Dipterocarpus caudiferus and a group of species on ultrabasic hills where the constant combination of the most frequent species consists of Shorea laxa, S. kunstleri, Dipterocarpus geniculatus, and D. lowii. Even more remarkable is that in East Sabah these species are restricted to ultrabasic areas while they occur in Southwest Sabah and adjacent Brunei and Sarawak on other geological formations and sandy clayish soils derived from these. A few species occur on the ultrabasic as well as on poor leached sandstone: Shorea venulosa and Shorea multiflora. Besides the edaphic-geological sorting of species there is variation in preferences according to drainage and altitudes (for examples, see Wood & Meijer, 1964), in a similar way as can be observed in Malaya and Sumatra. Shorea platyclados is the most prominent upper Dipterocarp-forest species in all three areas. Shorea curtisii, a mountain ridge species of Malaya and Sumatra, reaches into the southwest part of Borneo; Shorea monticola is a Crocker Range-Kinabalu species. Species like Hopea pentanervia and Dryobalanops beccarii are specialized to high level alluvium terraces with white sand and gravel along the upper Labuk River, in the Labuk delta, and around the Sook-plain. It is possible that all these white sands derive from an ancient Trusmadi, the second highest mountain in Sabah. The conclusion is that Dipterocarps have evolved in Borneo in all parts of the island between sea level and 6000 feet altitude in all kinds of habitats, most vigorously below 3000 feet. The present distribution centers of species are located in all parts of the island (Figs. 3-8). It looks as if given time, species could evolve anywhere. Having 50 species together within one forest, 20 species of Shorea within 80 acres (Fox, 1967), it seems unlikely that speciation can be explained by adaptation to different niches. Poore (1968) has tried to check that hypothesis in Malaya, but Wong and Whitmore (1970) could not substantiate it. My own impression from detailed sampling work is also that within one forest type species can have overlapping niches, slightly better drainage may benefit one species more than another, but where gaps occur in the forests when old trees fall over or rot away, it is often first come, first served, and among the mixture of seedlings and saplings coming up the one in the best position as regards light conditions will finally fill the gap in the canopy. The striking feature among some species with small areas is that they can

often be traced to their still living ancestors, so-called parent species which have larger areas of distribution. I am pretty sure that Parashorea malaanonan is the parent species of P. tomentella and that Shorea faguetiana is the parent of Shorea kudatensis. Other examples are given in Meijer (1963). A detailed computertaxonomy including data on phytochemistry, pollen structure, and wood anatomy could establish the taxonomic gaps between species and compare this with distribution areas. Ashton (1969) tried to explain speciation in Dipterocarps in the light of current theories of selection, adaptation, and genetic drift. He referred

back to a thought-provoking paper by Federow (1966), who tried to explain speciation in tropical rain forests through non-adaptive differentiation of small populations. Federow (1966) asserted that individuals of a population of a tree in a tropical forest are often spatially isolated, self fertilization must then be the rule. This is substantiated by sample plot studies by Poore (1964) in Malaya in which a survey was made of 23 hectares of forest in which among 381 species, 157 only occurred once. Of course, only the large-sized trees could be enumerated, and according to my experience a tree rare or scattered in one site might be much more frequent elsewhere. According to Ashton (1969) "the nature of the problem lends itself to speculation rather than scientific inquiry." His scholarly treatment cannot hide the fact that we know very little about actual selection pressures and adaptation in the life of Dipterocarps, though it becomes more and more clear now that crown structures and leaf forms may have far more adaptive strategic value than was thought before (Brunig, 1970). Also very little is known about pollination of dipterocarps. Ashton (1969) mentions the occurrence of the bees belonging to Apis dorsata in large nests in emergent trees of Koompassia excelsa in Malaya, Borneo, and Sumatra. In addition, we could mention the far greater frequency of occurrence of stingless bees belonging to the genus Trigona often living at the base of dipterocarp trees in nests made of resin of the trees. It is unlikely that pollinators can be very specific. Dipterocarp trees flower very infrequently at intervals of 3-5 or even 9 years. However, when they flower they flower in general gregariously, though

different species often in different phases (Wood, 1955; Meijer, 1967, 1974), and that could create isolation mechanisms (Fig. 2).

Fruit dispersal might be responsible for restricted areas of species as demonstrated by Ashton (1969) for a whole series of species often restricted to particular water catchment areas in Sarawak (Northwest Borneo). However, that does not necessarily prove that such species originated simply because of their spatial isolation between rivers acting as barriers to their dispersal. Therefore, I am strongly inclined to question Ashton's contention that the breeding pattern of Dipterocarps conforms to the normal pattern of speciation among pan-mictic herbaceous flowering plants. Fosberg (1970) points out that the floristic wealth of the lowland tropical rain forest is far greater than might be expected, considering the apparent uniformity of the rain forest environment.

Ecological isolation of species might have played a role in a genus like *Dryo-balanops* where each of the five Bornean species has its own ecological adaptive peak, but it looks different in *Shorea* with at least 150 species in Malaya, Su-

matra and Borneo; 60 in Malaya alone. It is impossible to imagine that they all occupy different ecological niches. I am inclined to leave options open for the possibility of speciation by saltation as suggested by Steenis (1969), in which one tree becomes the founder of a new species. After all, when a Dipterocarp flowers there are hundreds of thousands of flowers open on the crown of a tree and the bees swarming around these flowers will in general pollinate flowers on the same tree (Fig. 2). Some of our plots give an idea of the scattering of flowering crowns of two closely related species of *Parashorea* within 10 acres

MEIJER-PLANT GEOGRAPHIC STUDIES

of forest. In this case there is no evidence that the two species hybridize, though they flower at the same time.

I have found only one example of a dipterocarp hybrid—one between Dipterocarpus confertus and D. stellatus, mentioned in Wood and Meijer (1964) but overlooked by Ashton (1969) and Steenis (1969).

If a tree of *Parashorea malaanonan* underwent a mutation through radiation or any other cause which caused hairiness of leaves, longer size of stamens and a few other characters in a pleiotropic way, then this tree might become the

center of a new species, provided there is sufficient isolation between progeny of this tree and those belonging to the mother species. In this connection it should be noticed that species which can be of very scattered occurrence in one area are sometimes in other localities very gregarious. Examples: Shorea guiso very common around Darvel Bay, scattered around Sandakan Bay, Parashorea malaanonan is very dominant on basaltic soils near Mostyn, Labah Datu District. If we had more solid information on the migration rate of Dipterocarps, the rate with which the progeny of one tree can spread out to form a new population, we would have an idea of how long the areas of some of the endemic species in Sabah or Sarawak took to grow out from the "founder tree." In case we would assume that a dipterocarp can spread fruits and establish seedlings within a radius of one-eighth of a mile in 10 years' time, then it would take 8000 years to spread over a 100-mile radius. In case the large dipterocarp forests of Malesia are not wiped from the face of the earth within the next 20 years, we might still be able to collect more data on pollination, pollinators, exact phases and frequencies of flowering and fruiting, ecological adaptation of species and rate of dispersal and migration from a single tree as center. Meanwhile cytological studies as started by Jong and Lethbridge (1967) could give us more data on interspecific variation.

ISLAND HOPPING AND DISJUNCTIONS

Another way to study evolution in the dipterocarps is an analysis of disjunctions of genera and fragmentation of areas of species between the various islands and the Southeast Asian continent. The so-called Sunda shelf, including Malaya, Sumatra, and Borneo, has at least 25 species in common. One could be inclined to explain this by the fact that as recently as the Pleistocene these islands were connected. However, that depends on the length of the period of those land connections and the speed of migration of species. Far stronger differences are shown between Borneo and the Philippines in their dipterocarp floras. In the first place, the total number of species in the Philippines is only 52 (against around 300 in Borneo). The genus Dryobalanops represented with 5 species in Borneo is absent from the Philippines. Part of the species which the Philippines share with Borneo are most likely old, widespread: Dipterocarpus grandiflorus, D. gracilis, D. hasseltii, Anisoptera costata, Shorea gratissima, S. guiso. A few other shared species only occur in Borneo in areas adjacent to the Palawan and Sulu landbridges: Dipterocarpus warburgii and Vatica mangachapoi. This distribution is paralleled in other families, for example Flacourtiaceae.

It is, of course, possible that those with Eastern Borneo areas are relicts and were formerly far wider spread over the Sunda shelf. A case in point is Vatica mangachapoi, also reported from North Malaya (Ashton, 1969). We have to accept the fact that species may have died out. For example, in the genus Hopea there are no shared species except perhaps Hopea philippinensis, and it is unlikely that that one species is the source of the seven species of Hopea now known from the Philippines. The distribution of *Pentacme* with 2 species in the Philippines and others in Thailand shows that species must have died out in intervening areas. Much of the South China Sea between Indo-China, Borneo, and the Philippines might have been land sometime. In the genus Parashorea, which is represented in Sumatra by at least 6 species and in Malaya by 3, it looks as if the northeastern part of Borneo together with the Philippines forms a secondary center of speciation. Also within species distributions we can notice disjunctions. Anisoptera costata, a species of forests below 3000 feet altitude, is in Sabah and Brunei of very scattered occurrence (Ashton, 1969; Wood & Meijer, 1964). Nowhere in Sabah have I ever seen this species otherwise than as very isolated trees. In the 10,000 acres Sepilok Forest Reserve widely explored over a period of 9 years with frequent Forest School field classes, we found only a few isolated trees. There are no other species of dipterocarp with their principal region of distribution in western Malesia which extend as far eastwards as A. costata. It thus must be a very old species, and Slooten (1952) assumes that the origin of this and other Dipterocarpaceae of Malesia was somewhere in the region now occupied by the South China Sea. Possibly Anisoptera mindanensis of the Philippines is the same species (Slooten 1952: 10). From all the evidence known so far, it looks as if A. costata is in Borneo a rather senescent species. It has a low rate of regeneration and consequently it is now very scattered and rare. How much its "non-occurrence" in West Borneo is real or due to lack of exploration has still to be seen. The area of Dipterocarpus kerrii in Borneo is by no means a closed distribution pattern anymore (Fig. 7). In Sepilok Forest Reserve 15 miles west of Sandakan, we found one tree of this species within 10,000 acres, and maybe only on Jembongan Island is this species fairly common locally. It looks like a species on the way out. The same scattered occurrence can be noticed with Dipterocarpus gracilis. In Sabah it generally occurs as scattered individuals over the whole region. In Brunei it is very rare, only semi-gregarious in a few locations. In this case the senescence of this species could point to a former higher frequency during dry periods of the Pleistocene or earlier in the Pliocene as illustrated by Steenis (1961) and suggested by the former distribution of the mangrove genera Aegialitis and Camptostemon as shown by pollen analysis work of J. Muller (personal communication).

During the Pliocene these genera were fairly common in Borneo. Later on, *Aegialitis* disappeared and *Camptostemon* is now very rare in Borneo (Muller and Steenis *in litt.*). Possibly the contrasts between ultrabasic and sandstone Dipterocarp floras have to be explained also in terms of aggressive (strongly regenerating) versus non-aggressive species.

MEIJER-PLANT GEOGRAPHIC STUDIES

Parashorea malaanonan, Dryobalanops lanceolata, and Dipterocarpus caudiferus have not made much headway in Brunei and Sarawak-or have not reached there yet. Thus they left there ample space for Dipterocarpus geniculatus, Shorea laxa, and Shorea kunstleri, while in Sabah they invaded the new Tertiary deposits, especially the upper coastal marine platform before the forests on older geological formations got established on these. All these observations lead us to consider the possibility that gaps in distribution areas originated after periods in which one of the "older" widespread species were more gregariously distributed. Now assume we have the means to distinguish on the one hand new species with small areas and narrow taxonomic gaps from still living parent species and on the other hand "dying out" more isolated relict species. The whole picture becomes one of increasing diversity in the course of evolution, new species branching off from parent species, at first narrowly related, but with age having larger areas and wider systematic gaps-some species dying out or becoming fragmented; genera like Hopea, Shorea, Vatica, Anisoptera, and Dipterocarpus hopping over from Borneo to the Philippines. A few species in such genera little or not changed from their Bornean parent population; others branching off forming new endemic species.

I hope that from all this it will be clear that all possible attempts have to be made to maintain the Dipterocarpaceae as natural resources of Southeast Asia on a sustained yield basis, to set aside virgin Jungle Reserves for their continuous scientific studies, and to finance this research substantially. It is far more important to preserve these trees as *living monuments* for all time too come, than to remain content with our scrappy herbarium records and merely throw up our hands about the barbaric destruction of these natural resources by the military, by lumber-jacks, and by shifting cultivators.

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[VOL. 61

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818